

The Circumtropical Barnacle *Tetracitella divisa* (Nilsson-Cantell) (Balanomorpha, Tetracitidae): Cirral Activity and Larval Development

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T. divisa is reported for the first time from Australia (Magnetic Island, north Queensland). The functional morphology and cirral activity of the species resemble those of *Tetracitella purpurascens*, with emphasis on prolonged cirral extension in response to moderate water flow. Larvae brooded to the cyprid stage pass through 4 naupliar stages in the mantle cavity, showing vestigial limb setation and enlarged caudal papilla development. The cyprid undergoes further differentiation before release. The paradox of circumtropical insular distribution in spite of abbreviated free larval life (as a cyprid only) is discussed.

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INTRODUCTION

Tetracitella divisa is a small tetracitelline found under and between rocks in low intertidal habitats on tropical shores. The species, first described by Nilsson-Cantell (1921) from material collected in Sumatra and the Java Sea, was notable as the first balanomorph known to brood its embryos to the cyprid stage in the mantle cavity. Nilsson-Cantell gave a brief description of a brooded metanauplius and a description and figure of the cyprid.

Since its original discovery, *T. divisa* has been found in the Hawaiian Islands (Pilsbry, 1928; Edmondson, 1933; Ross, 1961), Formosa (Hiro, 1939), Kyusyu and Ryukyu Islands (Utinomi, 1949), South China Sea (Zevina and Tarasov, 1963), tropical west Africa (Bassindale, 1961; Stubbings, 1967), Dominica (Ross, 1968), India (Ross, 1971), Aldabra and Fiji (Foster, 1974). It thus has a circumtropical insular and occasional mainland distribution. Dense populations may occur, as in Fiji (Foster, 1974), where the species may cover up to 100% of available surfaces. B. A. Foster (pers. comm.) has also found *T. divisa* at Norfolk Island. The present paper reports the first discovery of *T. divisa* from Australia. Brooding to the cyprid stage in the mantle cavity was confirmed by Hiro (1939) and Ross (1961, 1968). Among other balanomorphs, this phenomenon has been described only in *Solidobalanus masignotus* (Henry and McLaughlin, 1967; Newman and Ross, 1971), and in a small tesseroporan from Hawaii (Newman and Ross, 1977) and various other Pacific islands (B. A. Foster, W. A. Newman, pers. comm.).

Some aspects of the anatomy of *T. divisa* were described by previous authors. The external appearance, wall plates and opercular plates were variously presented and figured by Nilsson-Cantell (1921), Hiro (1939), Ross (1961, 1968), Zevina and Tarasov (1963), Stubbings (1967) and Foster (1974). The individual mouthparts, though not the oral cone, were described by the same authors with the exception of Ross (1961) and were well figured by Stubbings (1967). Brief descriptions of the cirri, including podomere counts, were given by Nilsson-Cantell (1921), Hiro (1939), Zevina and Tarasov (1963) Stubbings (1967) and Ross (1968). The functional morphology and cirral activities of the species have not been investigated. Descriptions of development are also very brief,

being confined to the two stages given by Nilsson-Cantell (1921). In the present work, the opportunity is taken to describe the anatomy of the animal in more detail, to report on its cirral activities and to examine the sequence of development based on a full series of stages.

MATERIALS AND METHODS

Specimens were obtained from the undersurface of a coral boulder from the low intertidal of Picnic Bay, Magnetic Island, north Queensland in August 1982. The boulder was collected by Dr John Collins of the James Cook University of North Queensland, who presented the animals to me as a frequently occurring but unidentified species from that habitat.

Observations were made on the living animals, including an investigation of cirral responses to water currents generated across the aperture by means of a Pasteur pipette. The specimens were then fixed in 0.5% formalin-seawater (V/V). Anatomical investigations were carried out by dissection following the methods of Anderson (1981). Developmental stages found in the mantle cavities of 25 specimens were removed and transferred through alcohol to methyl benzoate, benzene and finally liquid paraffin. These specimens were studied microscopically as wet whole mounts in liquid paraffin.

RESULTS

The Anatomy of *T. divisa*

Wall and Operculum. Previous workers have described the wall plates and operculum of *T. divisa* in some detail. A resumé of these descriptions is given here, and illustrated from the Queensland material, as a preliminary to a more detailed consideration of structure and function.

The animal is of low conical shape in external view (Fig. 1A), with a basal diameter of 6-11mm. The basal margin of the wall is rounded in outline. There is a small, diamond-shaped to hexagonal orifice with a length about one quarter of the basal diameter. The four wall plates are distinct, with broad radii on the compound rostrum and laterals. The radii have horizontal summits and exhibit dark striations indicative of internal tubes. The external surface is covered by a pale brown chitinous cuticle marked by close set, imbricating growth lines fringed with fine chitinous hairs. Each plate may be strengthened by three or more ribs that protrude little or not at all beyond the margin. The parietes are penetrated by 2-6 rows of longitudinal tubes, quadrangular to hexagonal in cross section, filled with greyish mantle tissue. The basis is membranous, sometimes calcareous around the periphery only, or calcareous throughout. The internal space enclosed by the wall is small and subcylindrical. The ratio of external to internal basal diameter is approximately 2.3:1.

The yellowish operculum, set superficially within a shallow sheath, is of typical tetracelitelline form. In the closed position, the scuta occupy most of the orifice (Fig. 1A). Each scutum is long rostracarinally and short apicobasally (Fig. 1B). The external surface has a broad median depression. The internal surface (Fig. 1B) shows poor definition of the adductor muscle scar and adductor ridge, and there are no crests for the insertion of the rostral and lateral scutal depressor muscles. The articular ridge and furrow, however, remain broad and prominent. The tergum, as in other tetracelitellines, is short and wide (Fig. 1B), with a broad, shallow tergal spur clearly separated from the basiscutal angle and 4-8 crests for attachment of the tergal depressor muscles.

Little raising and rostral rotation of the opercular valves is involved in the opening of the aperture. The main movement is a lateral upswing of the valves on the hinge formed by the opercular membrane.

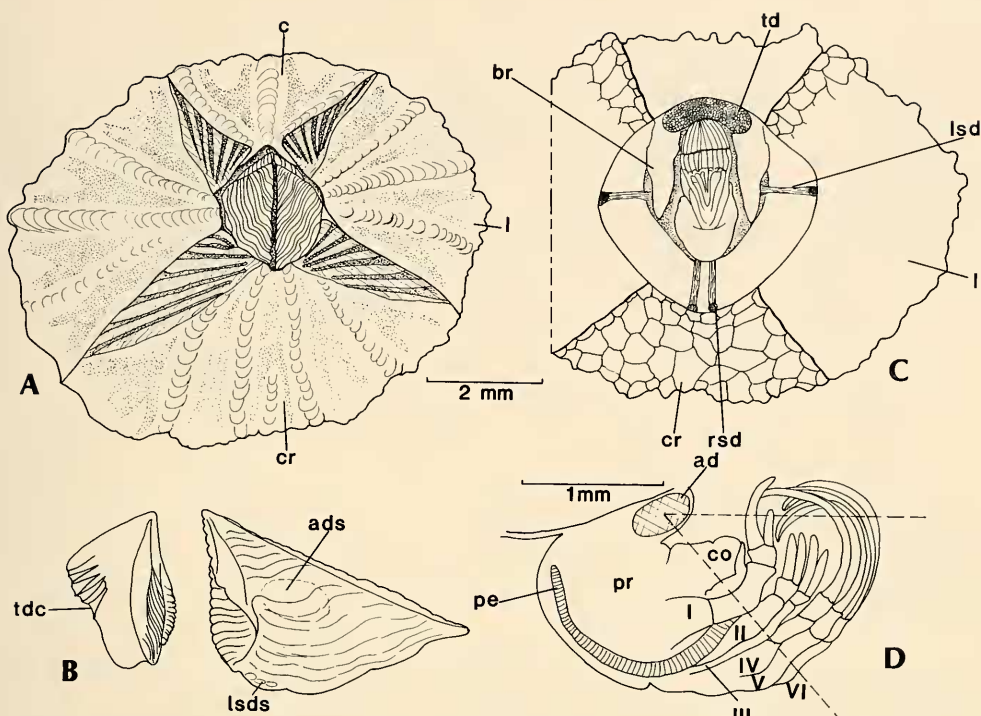


Fig. 1. *T. divisa*. A. — External apical view. B. — Right scutum and tergum, anterior view. C. — Basal view. D. — Body and limbs, right lateral view. *ad*, adductor scuturum; *ads*, adductor scuturum scar; *br*, branchia; *c*, carina; *co*, oral cone; *cr*, compound rostrum; *l*, lateral; *lsd*, lateral scutal depressor muscle; *lsds*, lateral scutal depressor scar; *pe*, penis; *pr*, prosoma; *rsd*, rostral scutal depressor muscle; *td*, tergal depressor muscle; *tds*, tergal depressor muscle crests; I-VI, cirri I-VI.

Body, Mantle Cavity and Depressor Muscles. Commensurate with the low profile of the wall and the small interior space, the body of *T. divisa* shows the typical long, low configuration of a tetracitelline (Fig. 1D) and is small relative to the size of the animal as a whole (Fig. 1C). The prosoma protrudes well forward of the level of the adductor scuturum, to occupy the rostral part of the mantle cavity. A pair of long, pointed branchiae lies lateral to the body and limbs. The paired tergal depressor muscles are large and fill the carinal end of the mantle cavity. The lateral and rostral scutal depressor muscles are thin.

Cirri. The cirri are not well described in previous accounts, but conform to the general tetracitelline pattern. The maxillipeds (cirri I-III) have short rami, while those of the captorial cirri (IV-VI) are of moderate length.

Cirrus I (Fig. 2A) has a long, curved protopod and an exopod of 8-10 podomeres, recurved carinally. The exopod carries apically directed, serrulate setae on the median face and tip. The shorter endopod of 4-6 podomeres also has serrulate setae, but these are directed posteriorly. Four long, serrulate setae project postero-apically from the basis.

Cirrus II (Fig. 2B) has a long protopod but short rami, the exopod having 6-8 and the endopod 5-7 podomeres. The serrulate setae of the protopod and both rami are directed anteriorly, except for a sparse, postero-apically directed fringe along the posterior margin of each ramus. The apical podomere of each ramus also carries several forwardly

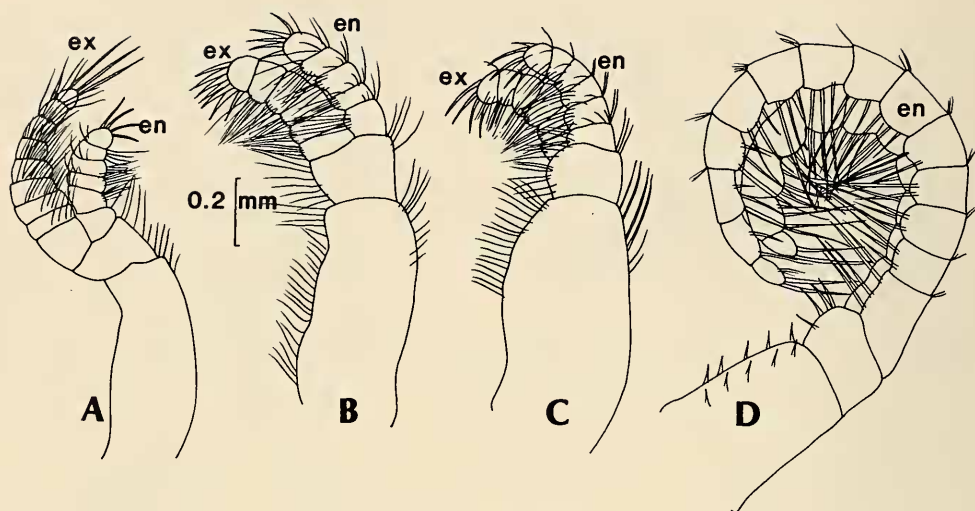


Fig. 2. *T. divisa*. A-E. — Left cirri in median view. A. — Cirrus I. B. — Cirrus II. C. — Cirrus III. D. — Cirrus V. *en*, endopod; *ex*, exopod.

curved, serrate setae with a double row of heavy setules along the concave margin. A few pappose setae project from the postero-apical corner of the coxa and basis.

Cirrus III (Fig. 2C) is slightly shorter than cirrus II, with a broad protopod as well as short rami. The exopod and endopod have 6-7 and 5-7 podomeres respectively. Setation is similar to that of cirrus II, except for an additional intermixture of serrate setae among the anteriorly pointing, serrulate setae of the endopod.

Cirri IV-VI (Fig. 2D) are typical captorial cirri. Representative podomere numbers are 13/11, 15/13 and 15/14 for the exopod and endopod. The podomeres carry 2 long pairs and 1 short pair of serrulate setae anterolaterally. The protopod carries sparse anterior spines.

Mouthparts. The general configuration of the oral cone has not been described for *T. divisa*. The individual mouthparts have been well described and figured by previous workers (e.g. Hiro, 1939; Stubbings, 1967).

The oral cone (Figs 3A, 3B) is low and wide and the labrum is only weakly bullate. In posterior view, the large, obliquely inclined mandibular palps obscure the labrum. Curved setae on each palp fringe the entrance to the preoral cavity. The short maxillae are set well on to the dorsal surface of the oral cone and point more posteriorly than ventrally.

The labrum (Fig. 3C) has a shallow median indentation on the posterior margin, with 3-4 low protuberances and a fringe of short hairs on either side. The long mandibular palps have serrulate setae apically and a fringe of jointed setae along the median edge. The mandible (Fig. 3D) is quadridentoid, with a prominent incisor tooth and subsidiary cusps on the 2nd-4th teeth. The molar process carries a group of 4 sharp spines of variable length. The maxillule (Fig. 3E) has two large and two small spines above a small notch. 6-8 spines occupy the cutting edge below the notch, and a group of smaller spines occupies the median angle. The maxilla (Fig. 3F) is typical, with an apical lobe carrying serrulate setae and a proximoventral lobe with jointed setae.

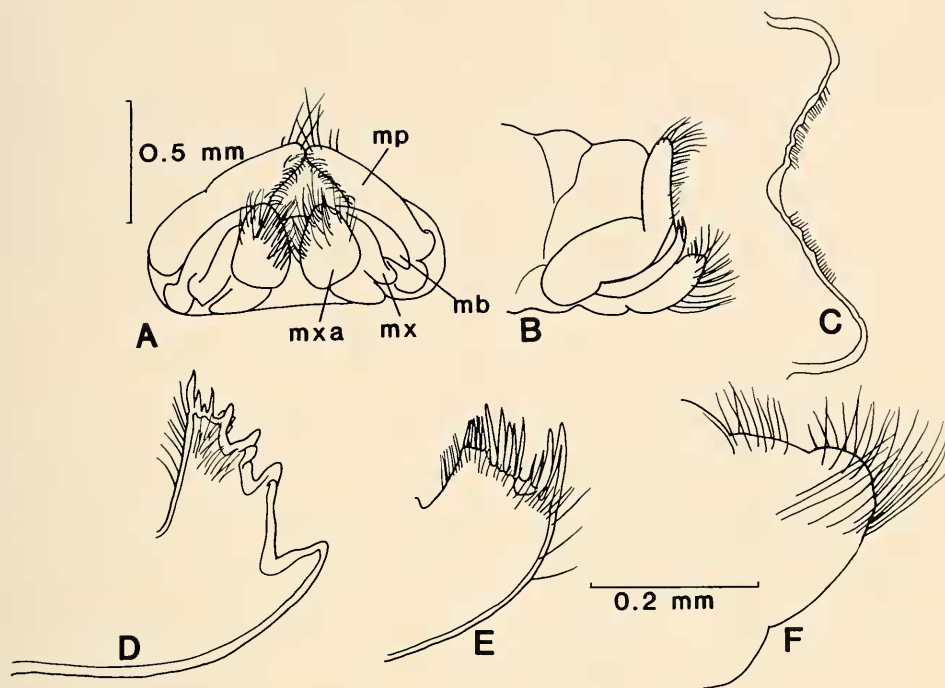


Fig. 3. *T. divisa*. A and B. — Posterior and right lateral views of oral cone. C. — Labrum, ventral view. D. — Right mandible, lateral view. E. — Right maxillule, lateral view. F. — Left maxilla, median view. *mb*, mandible; *mp*, mandibular palp; *mx*, maxillule; *mx**a*, maxilla.

Cirral activity in *T. divisa*

Prior to cirral activity, the small opercular valves swing open at a low angle, with very little uplift. In still water, the opercular valves are held open and pumping beat commences. The curled long cirri emerge slightly above the carinal end of the aperture on each beat. The exopods of the first cirri also emerge, apposed and upright, in front of the long cirri. The pumping beat becomes more active in response to mechanical vibration induced by light tapping on the rock surface adjacent to the animal.

The application of a gentle water current across the orifice immediately evokes prolonged cirral extension. The cirral fan is held upright as long as the water current flows. Rotation of the extended fan up to 70–80° in either direction occurs in response to water currents impinging on the animal either laterally or carinally. Responses to stronger currents were not investigated.

Larval development in *T. divisa*

As mentioned above, only Nilsson-Cantell (1921) described any of the developmental stages of the larvae brooded in the mantle cavity of *T. divisa*. He distinguished a metanauplius stage, 0.84mm long, with a rounded body and well developed thoracic limb rudiments. The larva retains the three pairs of naupliar limbs, but with reduced setation. The second stage described by Nilsson-Cantell was the cyprid, 0.62mm long,

with a typical bivalve carapace, eyes and antennules, but with a prominent thoraco-abdominal process.

The present material has yielded a longer sequence of stages which reveal the major progression of development. The embryos, deposited in the mantle cavity as paired adherent masses, are not embedded in typical gelatinous lamellae. Early embryos are brownish, yolk-filled and ovoid, with diameters of $450 \times 350 \mu\text{m}$. Within the egg membrane, embryonic development proceeds with little increase in volume, yielding naupliar limb rudiments and a small caudal papilla (Fig. 4A). These rudiments become more conspicuous, and a median eyespot develops anteriorly. The embryo then hatches from the egg membrane, freeing the naupliar limbs, and changes slightly in shape (diameters $450 \times 330 \mu\text{m}$). The body of the hatched, embryonized nauplius remains yolk-filled (Fig. 4B). The naupliar limbs are simple, with short, vestigial setae at the tip of each limb. The antennae are slightly longer than the antennules and mandibles.

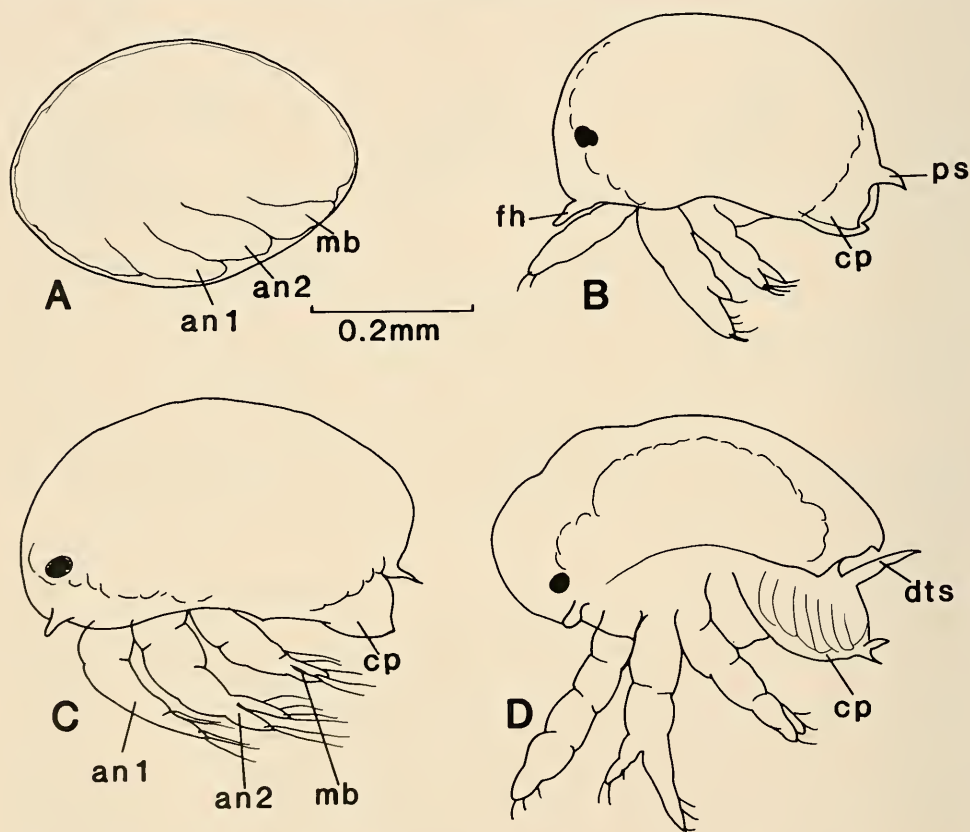


Fig. 4. *T. divisa*. A-D. Developmental stages from the mantle cavity. A. — Embryo before hatching. B. — Stage I nauplius; C. — Stage II nauplius. D. — Stage III nauplius. *an1*, antennule; *an2*, antenna; *cp*, caudal papilla; *dts*, dorsal thoracic spine; *fh*, frontolateral horn; *mb*, mandible; *ps*, posterior shield spine.

The first stage nauplius increases in volume and undergoes a moult to a second stage (Fig. 4C) in which the caudal papilla becomes more prominent. The antennae and mandibles develop more clearly bifid tips. At the second moult, the third stage nauplius (Fig. 4D) shows considerable enlargement of the caudal papilla and a dorsal thoracic spine, reduction of the posterior shield spine and some reduction in the volume of yolk

within the body. The lateral margins of the dorsal shield are now sharply delineated and the setation of the limbs is reduced. During this stage, the caudal papilla begins to show signs of segmentation. Another moult then follows, yielding a fourth stage nauplius (Fig. 5A), the last before the cyprid. The caudal papilla is further enlarged, while the naupliar limbs show a reduction in the number of vestigial setae. Paired compound eyes develop anteriorly and paired, setose thoracic limbs are conspicuous in the caudal papilla. The outline of the body changes towards that of a more typical, late stage tetracelitid nauplius, with a broad straight front. Internally, the outlines of internal organs become defined, although much yolk remains.

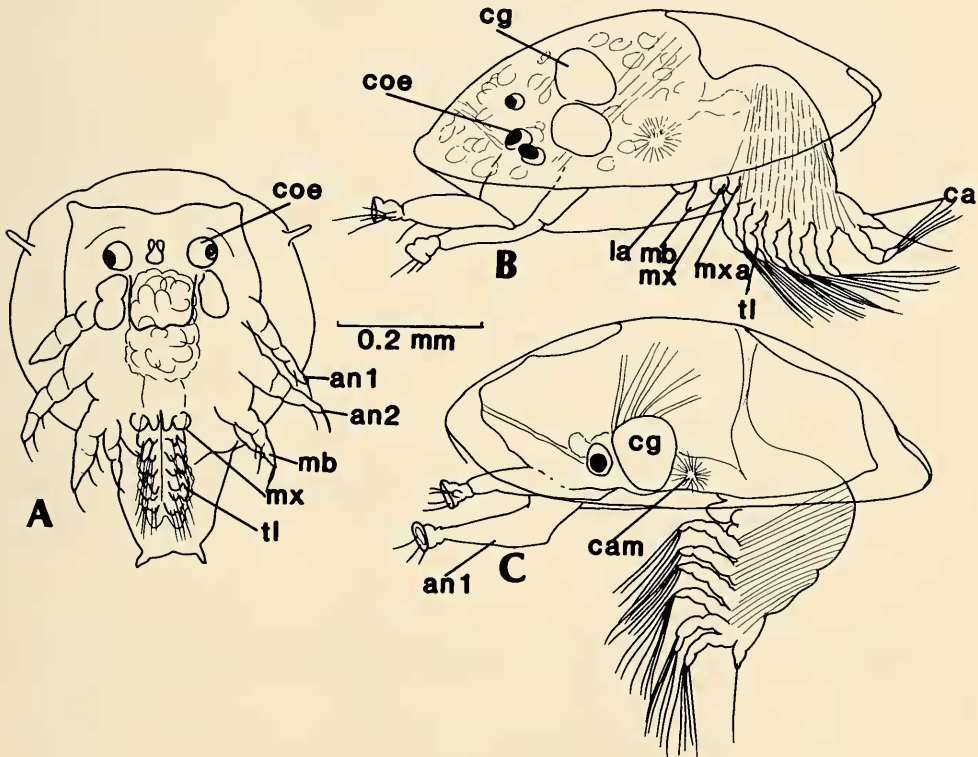


Fig. 5. *T. divisa*. A-C. — Later developmental stages from the mantle cavity. A. — Stage IV nauplius; B. — Early cyprid. C. — Late cyprid. *an1*, antennule; *an2*, antenna; *ca*, caudal appendage; *cam*, cyprid adductor muscle; *cg*, cement gland; *coe*, compound eye; *la*, labrum; *mb*, mandible; *mx*, maxillule; *mx*, maxilla; *tl*, thoracic limbs.

The young cyprid, apart from the continuing yolk content, is of the usual cyprid structure (Fig. 5B). As the cyprid continues its development and the yolk is used up, (Fig. 5C), the 6 pairs of setose thoracic limbs and their musculature become fully differentiated and the compound eyes and cement glands become more conspicuous, but there is still little sign of development of the gut. The 3 pairs of mouthpart rudiments are obvious but not functionally differentiated. Cyprids must escape the mantle cavity at this stage, but it seems likely that free-swimming life is brief. Little reserve material remains within the larva, and feeding is not possible.

DISCUSSION

Functional Morphology. Anderson and Anderson (1985), studying *Tetraclitella purpurascens*, drew attention to the many generalized balanomorph features retained in the Tetraclitellinae, some of which had already been recognized by Ross (1969). They include a low conical profile maintained by diametric growth: associated broad radii; weak articulation of the wall plates; a flattish operculum with large tergal depressor muscles, small scutal depressor muscles and no scutal depressor muscle scars; a small mantle cavity with little free space for respiratory flow; an elongate prosoma and thorax with limbs in serial array; short maxillipeds, but a high, narrow oral cone. Anderson and Anderson also showed that the diametric growth of the tetraclitelline wall is based on a unique specialization, open-sided tubiferous parietes capable of circumferential growth. This feature was figured by Hiro (1939) but its significance in promoting rapid diametric growth has only recently been appreciated.

The same pattern of morphological organization, except for a lower profile to the oral cone, is displayed by *Tetraclitella divisa*, at a much smaller maximum size than *T. purpurascens*. Concomitantly, the two species share a common mode of opercular and cirral activity. Anderson and Buckle (1983) observed that *T. purpurascens* performs respiratory pumping beat in still and slowly flowing water, and responds to moderate external water flow by prolonged cirral extension. Anderson and Anderson (1985) found that the opercular movements associated with these cirral activities in *T. purpurascens* are simple, involving a hinge-like opening and closing action on a thick opercular membrane, with only moderate uplift. *T. divisa* exhibits similar opercular movements, performs respiratory pumping beat in still water and enters into prolonged cirral extension in response to slow to moderate external water flow. Both species also have a limited rotational capacity of the extended cirral fan, to not more than 90° in either direction.

Thus in spite of obvious differences in size and distribution, *T. divisa* and *T. purpurascens* epitomize a functional organization that is probably characteristic of all tetraclitelline species, combining a generalized balanomorph pattern of respiration and feeding with a hypobiontic habit and a capacity for rapid diametric growth. Further studies on other species of *Tetraclitella* from this point of view would be of particular interest.

Larval Development. In the light of the morphological conservatism of the tetraclitellines, the unusual modifications of larval development in *T. divisa* are particularly striking. Embryonic and larval development described in some other species of the genus follow the characteristic balanomorph mode, with eggs of moderate size (approx. 200µm) hatching as typical stage I nauplii and passing through the usual sequence of six planktotrophic naupliar stages followed by a cyprid stage (Anderson, 1969; Karande, 1974, 1982; Barker, 1976; Egan and Anderson, in preparation). *T. divisa* has a secondarily enlarged, yolky egg (450×350µm), hatches as a lecithotrophic stage I nauplius with vestigial setation, remains within the mantle cavity throughout its lecithotrophic development to the cyprid stage and is free-swimming only as a cyprid. During this brooded development, the number of moults is reduced, yielding only four naupliar stages before the cyprid. The naupliar limb setation remains vestigial in all naupliar stages, and the main emphasis is on development of a large caudal papilla. Some yolk still remains when the moult to the cyprid takes place, and the cyprid undergoes considerable further differentiation at the expense of this yolk, including functional elaboration of the antennules, the thoracic limbs and their musculature, and the cement glands, before reaching the stage of release. Development of the cyprid organization is thus a more direct and gradual process in *T. divisa* than in typical planktotrophic balanomorph larvae. Convergently similar modifications towards direct development through

a reduced number of lecithotrophic naupliar stages, followed by release from the mantle cavity at the cyprid stage, have been noted in the lepadomorph *Ibla idiotica* (Batham, 1945) and in most Acrothoracica (Turquier, 1972, 1985). The developmental sequences in the two other balanomorphs known to release their larvae at the cyprid stage have not yet been described.

Distribution. As pointed out by Newman and Ross (1977), the distribution of *T. divisa* presents a paradox. The species is circumtropical and mainly insular, occurring as a series of widely separated, geographically isolated, intertidal populations. At the same time its planktonic larval phase is very abbreviated. The present work indicates that the cyprid retains no yolk reserves when released, and is like other cyprids in being unable to feed. Settlement in the vicinity of the adult population is thus favoured, resulting in the known build-up of dense local populations; but dispersal as planktonic larvae over long distances is not possible. The circumtropical insular distribution therefore suggests oceanic transport on floating objects, for which some evidence was provided by Newman and Ross (1977). On arrival at a suitable location, the mode of cyprid release would facilitate rapid colonization, in a manner analogous to that of many ascidians with brood retention and abbreviated larval life. The selective forces that led a few, scattered balanomorph species into this mode, however, with its increased egg size and consequent modifications towards direct development, remain a mystery.

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